

# Responses of switchgrass soil respiration and its components to precipitation gradient in a mesocosm study

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## Abstract

**Aims** The objective of this study was to investigate the effects of the precipitation changes on soil, microbial and root respirations of switchgrass soils, and the relationships between soil respiration and plant growth, soil moisture and temperature.

**Methods** A mesocosm experiment was conducted with five precipitation treatments over two years in a greenhouse in Nashville, Tennessee. The treatments included

ambient precipitation,  $-50%$ ,  $-33%$ ,  $+33%$  and  $+50%$  of ambient precipitation. Soil, microbial, and root respirations were quantified during the growing seasons.

**Results** Mean soil and root respirations in the  $+50%$  treatment were the highest ( $2.48$  and  $0.93 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , respectively) among all treatments. Soil microbial respiration contributed more to soil respiration, and had higher precipitation sensitivity mostly than root respiration. Increases in precipitation mostly enhanced microbial respiration while decreases in precipitation reduced both microbial and root respirations. Across precipitation treatments, soil respiration was significantly influenced by soil moisture, soil temperature, and aboveground biomass.

**Conclusions** Our results showed that microbial respiration was more sensitive to precipitation changes, and precipitation regulated the response of soil respiration to soil temperature. The information generated in this study will be useful for model simulation of soil respiration in switchgrass fields under precipitation changes.

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## Introduction

Soil respiration, the combined respiration of living roots and soil microbes, is one of the largest fluxes in the global carbon (C) cycle (Schlesinger and Andrews 2000; Hui and Luo, 2004; Deng et al. 2012). Soil respiration plays an important role in soil C sequestration (Raich and

Schlesinger 1992), and is often sensitive to changes in temperature and precipitation (Luo et al. 2001; Deng et al. 2012; Vicca et al. 2014). Due to the CO<sub>2</sub> emissions from fossil fuel combustion, the global land surface temperature has increased over the past decades (IPCC 2013). Researchers predict alterations in the Earth's water cycle, including changes in precipitation pattern and amount to produce more extreme precipitation events (Huntington 2006). More drought or wet years in the United States would be expected in the future (IPCC 2013).

Bioenergy crops are expected to become widespread in the next several decades (McLaughlin and Kszos 2005). Switchgrass (*Panicum virgatum* L.) is a perennial C<sub>4</sub> grass and was one of the most dominant species in the North America prairie ecosystems (Weaver and Fitzpatrick 1932; McLaughlin and Kszos 2005). Switchgrass is a candidate for bioenergy cropping because it can tolerate soil water and nutrient deficits and grow in marginal lands (Gelfand et al. 2013). The high productivity of switchgrass gives it potential to increase soil C sequestration (McLaughlin and Kszos 2005). However, the contribution of soil respiration to carbon cycling in bioenergy cropland including switchgrass has not been well investigated, and it is urgent to know how precipitation change would influence soil respiration in switchgrass croplands.

Effects of climate change on soil respiration in native grasslands have been extensively investigated over the past decades (Raich and Tufekciogul 2000; Hartman et al. 2012). Seasonal changes in soil respiration are strongly affected by soil temperature and soil moisture (Singh and Gupta 1977; Xu and Baldocchi 2004; Craine and Gelderman 2011; Gritsch et al. 2015). In general, increases in soil temperature and soil moisture can enhance soil respiration (Singh and Gupta 1977; Wen et al. 2006; Yuste et al. 2007), as activities of soil microorganisms and plant roots are often stimulated (Raich and Potter 1995; Qi et al. 2002). The responses of root respiration to temperature and moisture may differ among various vegetation types (Atkin et al. 2000). Partitioning of soil respiration into its root and microbial components has rarely been done for switchgrass, but are valuable for understanding their contributions to C cycling in switchgrass crops.

In switchgrass fields, soil respiration rates increase as temperatures increase through the growing season, and to a greater extent at higher soil moisture levels (Wagle and Kakani 2014). Change in precipitation or soil moisture may also influence temperature sensitivity of soil

respiration (Q<sub>10</sub>) (Davidson and Janssens 2006; Qi et al. 2002; Wagle and Kakani 2014). Average of soil respiration from 5 to >13 μmol m<sup>-2</sup> s<sup>-1</sup> has been reported in switchgrass field (Huang et al. 2016). But most of previous studies only focused on total soil respiration. The separate contributions of microbial and root respirations to the temperature and precipitation sensitivities of switchgrass under different precipitation treatments need to be investigated.

This study was designed to determine the effects of sustained precipitation changes on soil respiration and its microbial and root respiration components in switchgrass soils. Specifically, we tested 1) whether there were any significant effects of the precipitation treatments on the soil, microbial and root respirations of switchgrass soils, and 2) how soil, microbial and root respirations were related to plant growth or soil moisture and soil temperature.

## Materials and methods

### Experimental design

The pot experiment was conducted in a greenhouse at Tennessee State University Agricultural Research and Education Center (AREC, Latitude 36.12°N, Longitude 86.89°W, Elevation 127.6 m) in Nashville, Tennessee. The greenhouse was constructed with roof and wall panels which could open or close in response to maintain predetermined conditions of temperature and humidity. Roofs and wall panels opened automatically when air temperature was above 20 °C and there was no rain; roofs automatically closed at threat of, and during rain. On July 13, 2013, five plants of two-year old "Alamo" switchgrass from a field experiment at TSU AREC were transplanted into 95 L. pots (50 cm diameter and 50 cm height) in the greenhouse containing Armour silt loam soil (pH = 6.2) also collected from the field experiment. No fertilizers were applied during this study. During establishment pots were watered in the ambient pattern described below. Plants were harvested three times in a year, at the beginning of May, Aug, and Nov each year, resulting in three harvest periods (Feb–April; May–July; Aug–Oct) during the growing season.

Five precipitation treatments were applied to the pots in a completely randomized block design with five blocks. Treatments were: ambient precipitation, two

drought treatments (−33% and −50% of ambient precipitation), and two wet treatments (+33% and +50% of ambient precipitation). The ambient precipitation treatment was based on the precipitation record from 1969, which closely matched the long-term (1913–2012) precipitation record in total and monthly amounts at Nashville, TN (Supplemental Document Fig. S1). The precipitation treatments started on Feb 1, 2014. Water was added 3 times per day, 10 days per month (2014) or 2 times per day, 10 days per month (2015) in amounts that summed to the prescribed monthly total. Wetter/dryer treatments were achieved by lengthening or shortening individual application duration. The precipitation treatments were applied using a watering timer controller (RSC600i, Raindrip, Inc. Woodland Hills, CA). In June and July of 2015, two incidents of failed roof control caused several pots to receive natural precipitation. We reduced irrigation for those pots after the rain.

#### Soil temperature, moisture, respiration, and plant growth measurements

Soil temperature and moisture sensors (Watermark Monitor 900 M, IRRMETER Inc., Riverside, CA) were buried at 20 cm depth in each pot near soil collars (see below) to continuously monitor soil temperature and moisture. The data were recorded every hour. The soil moisture sensor measures soil matric potential in centibar (cb), which is equal to  $10^{-3}$  megapascal (MPa), over a range of 0 to 239 cb (Irmak and Haman 2001).

Soil respiration and soil microbial respiration were measured monthly using the Li-6400 connected to a soil chamber (LiCor Inc., Lincoln, NE, USA). Soil respiration was measured at two polyvinyl chloride (PVC) soil collars (10 cm diameter, 5 cm height) permanently inserted in each pot prior to planting with 2 cm of the collars remaining above the soil surface. To measure soil microbial respiration, a larger soil collar (20 cm diameter and 30 cm height) was installed to exclude root growth in the collar in two blocks. A third soil collar (10 cm diameter, 5 cm height) was set inside this collar and soil respiration measured from this third collar was considered as soil microbial respiration. Root respiration was estimated as the difference between soil respiration and soil microbial respiration.

The maximum plant height in each pot was measured on the tallest tiller at the end of each harvest period. Aboveground biomass was measured by harvesting all

above-ground tillers from the pot, drying them at 75 °C for 24 h, and weighing.

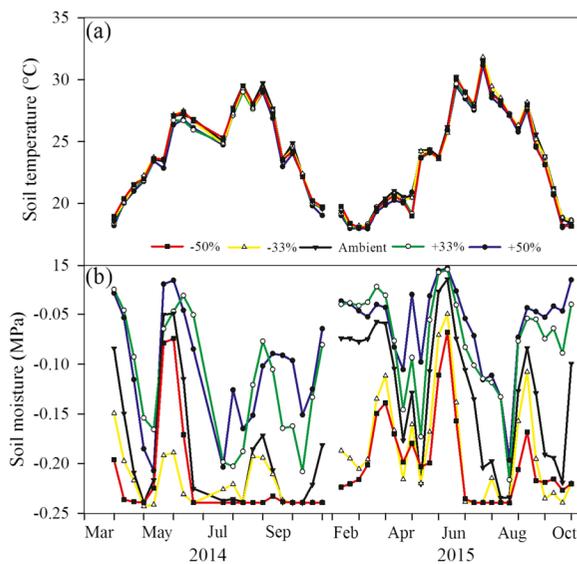
#### Statistical analysis

Data analysis was performed using SAS software 9.3 (SAS Inc. Cary, NC; Hui and Jiang 1996). The effects of precipitation treatment, year, harvest period and block on soil moisture, soil temperature, soil respiration and microbial respirations were analyzed using repeated measure analysis of variance (ANOVA). When a significant effect was detected, least significant difference (LSD) was used for multiple comparisons. To develop precipitation sensitivity of soil respiration, linear regression model was applied to soil, microbial, and root respiration with precipitation amount. Significant test of precipitation sensitivity (i.e. slope of linear regression model) between years and among harvest periods was conducted using the homogeneity of slope model. Student t test was used to test the significance of slopes between soil microbial and root respiration. Multiple regression analysis was conducted to develop the relationships of soil, microbial and root respirations with aboveground biomass, tiller height, soil temperature, and soil moisture under all treatments. We first checked whether there was a significant relationship between soil respiration and each of these independent variables (bivariate regression). Multiple regression with stepwise selection was then conducted to select the model variables (Hui and Jiang 1996). Variable significant at 0.05 level was entered into model and variable not significant at 0.05 level was removed from the model. Non-linear regression analysis (an exponential equation,  $R = R_0 \exp.(bT)$ ) was conducted to link soil respiration (R) with soil temperature (T) under different precipitation treatments, and estimate the temperature sensitivity of soil respiration  $Q_{10} = \exp(10b)$  (Deng et al. 2012).

#### Results

##### Seasonal variations of soil temperature, moisture and soil respiration among precipitation treatments

There were strong seasonal variations of soil temperature in both growing seasons, with high temperature during summer (Fig. 1a). The highest daily soil temperature was



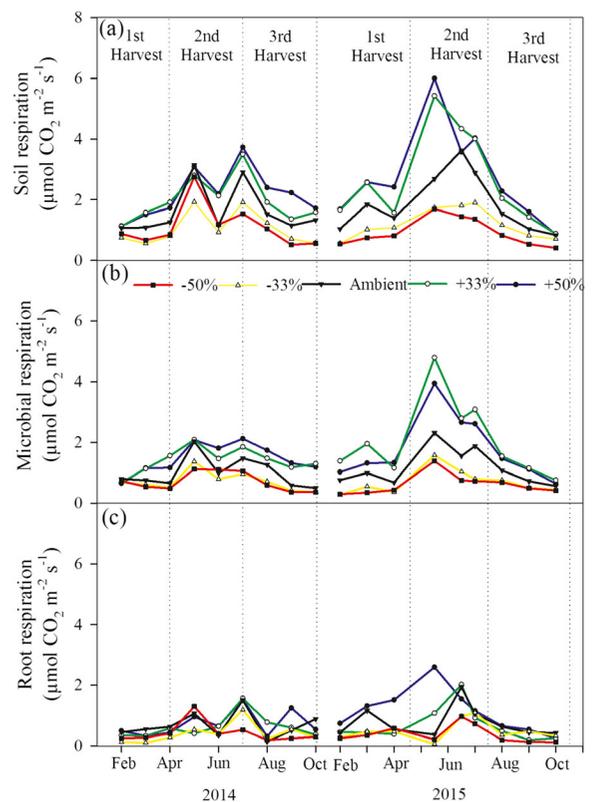
**Fig. 1** Monthly mean soil temperature (a) and moisture (b) in each precipitation treatment from Feb to Oct in 2014 and 2015

29.2 °C in 2014 and 31.2 °C in 2015. Precipitation treatments had no significant influence on soil temperature. Soil moisture in both growing seasons varied with the precipitation treatments (Fig. 1b). The soil moisture linearly increased with stimulated precipitation (Supplemental Document Fig. S2). Soil moisture decreased with the decrease of the amount of water applied. Soil moisture in the +33% and +50% treatments was higher than that in the -33% and -50% treatments.

Soil, microbial, and root respiration rates generally increased and reached the highest values in July or June, and declined towards the end of the growing seasons (Fig. 2). Mean total soil respiration rates ranged from 0.41 to 5.85  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . The seasonal dynamic patterns of soil, microbial, and root respirations were similar for all treatment, but the magnitudes of +50% and +33% treatments were mostly higher than these of other three (ambient, -33% and -50%) treatments. In addition, the rates of soil, microbial and root respirations in 2015 were higher than that in 2014.

Significant tests of precipitation treatment, harvest period, year and their interaction

Results of ANOVA showed that soil and microbial respiration rates were significantly affected by precipitation treatment, harvest period, and year (Table 1). Significant interactive effects between precipitation treatment and



**Fig. 2** Monthly mean soil respiration (a), microbial respiration (b), and root respiration (c) in each precipitation treatment from Feb to Oct in 2014 and 2015. Sample size is 10 for root and microbial respiration, and 25 for soil respirations

harvest period or between precipitation treatment and year were found for soil and microbial respirations.

Effects of precipitation treatment on switchgrass soil, root, and microbial respiration rates

The precipitation treatments significantly influenced soil, microbial and root respiration rates (Fig. 3). Among all treatments, the +50% treatment had the highest soil respiration rate (2.54  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ). Soil respiration was significantly lower in the +33% treatment and further decreased in the ambient treatment. The lowest soil respiration rates appeared in two drought treatments, with no significant difference between the -33% and -50% treatments. Microbial respiration contributed more to total soil respiration than root respiration (Fig. 3), with mean microbial respiration about twice that of root respiration. The highest microbial respiration (1.74  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) appeared in the +33% treatment, and was lower in the ambient

**Table 1** Significance of the effects of precipitation treatment, harvest period, their interactions on soil respiration and microbial respiration in two years using repeated measure ANOVA

Source	df	Soil respiration ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	df	Microbial respiration ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )
Block	4	6.50**	1	8.62**
Precipitation	4	421.70**	4	135.66**
Year	1	202.94**	1	25.97**
Harvest	2	1061.06**	2	283.31**
Precipitation*Harvest	8	26.75**	8	8.97**
Precipitation*Year	4	36.03**	4	11.52**

Numbers are F values

Stars indicate the level of significance (\* =  $p < 0.05$ , \*\* =  $p < 0.01$ )

( $1.11 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ),  $-33\%$ , and  $-50\%$  precipitation treatments ( $0.70$  and  $0.66 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , respectively). The  $+50\%$  treatment increased root respiration, and the  $-50\%$  treatments significantly decreased root respiration.

Variations in soil, root and microbial respiration rates between the two years

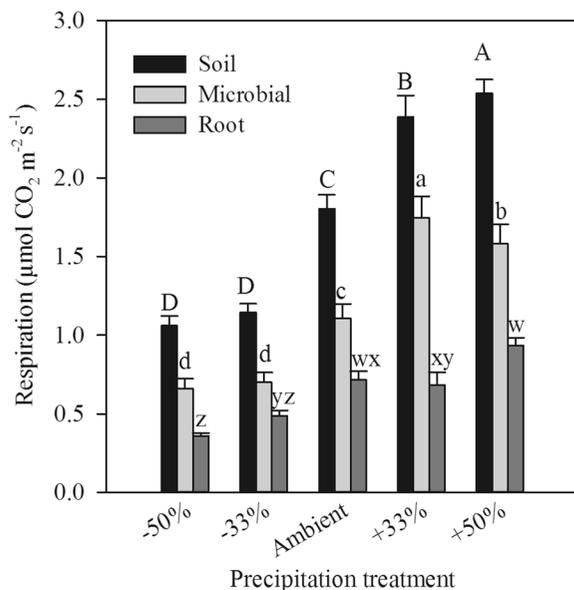
Soil and microbial respiration rates showed significant differences between the two years (Table 2). Soil, microbial, and root respirations ( $2.01$ ,  $1.23$ , and  $0.71 \mu\text{mol}$

$\text{CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , respectively) were higher in 2015. Considering there were significant interactions between precipitation treatment and year, we further looked at the effects of precipitation treatment in each year. To quantify the change in soil, root and microbial respirations to precipitation change, we developed the relationships of respiration and simulated precipitation amount (Fig. 4; Table 3) in 2014 and 2015. Although soil respiration seemed to decrease less under lower precipitation, linear regression models were best optimal models for both years. The slope of linear regression model was an indicator of precipitation sensitivity. Precipitation sensitivity of soil respiration was significantly higher in 2015 than 2014, but precipitation sensitivities of microbial and root respirations showed no significant differences between the two years (Fig. 4; Table 3). Soil microbial respiration was more sensitive to precipitation change than root respiration. Increased precipitation increased total soil respiration more by increasing the contribution of microbial respiration.

Variations in soil, root and microbial respiration rates among the three harvest times

Significant differences in soil, microbial and root respirations were also observed among the three harvest periods (Table 4). The rates of soil, microbial and root respirations ( $2.70$ ,  $1.75$ , and  $0.99 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , respectively) were higher in the 2nd harvest period (May-Jul).

Precipitation sensitivity of soil, microbial, and root respirations was also highest in the second harvest period, and precipitation sensitivity of microbial respiration was higher than root respiration in all three periods (Fig. 5;



**Fig. 3** Multiple comparison of soil, microbial, and root respiration rates among different precipitation treatments. Error bars are standard errors

**Table 2** Multiple comparisons of soil, microbial and root respiration rates of switchgrass soils between two years

Year	Soil respiration ( $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$ )	Microbial respiration ( $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$ )	Root respiration ( $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$ )
2014	$1.59 \pm 0.06^a$	$1.05 \pm 0.03^a$	$0.57 \pm 0.05^a$
2015	$2.01 \pm 0.09^b$	$1.27 \pm 0.05^b$	$0.71 \pm 0.07^a$

Data are mean  $\pm$  SE. The sample size is 225 for soil respiration and 90 for microbial and root respiration. LSD is used for multiple comparison between means. Different letters indicate significant differences between two years

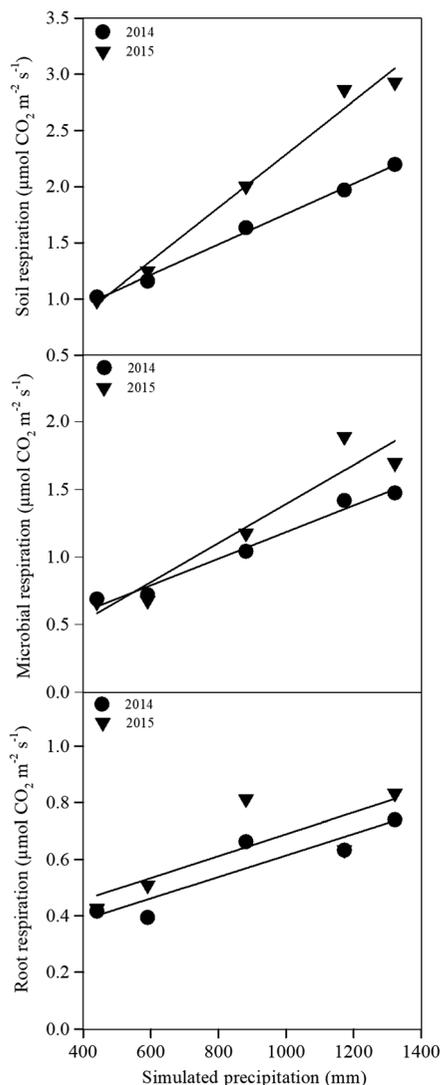
Table 3). Soil respiration increased by  $0.079 \mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$  as precipitation increased by 1 mm on average in

the 2nd harvest period, but only  $0.043$  and  $0.037 \mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$  in the 1st and 3rd period, respectively. Similar trends were found for soil microbial and root respirations.

Relationships among soil, root, and microbial respiration rates and plant growth, soil temperature, and soil moisture under all precipitation treatments

Soil, microbial and root respiration rates showed linear relationships with soil temperature, soil moisture and aboveground biomass (Fig. 6). It seems that aboveground biomass contributed most, and explained 66%, 79%, and 61% of soil, microbial, and root respiration, respectively. Soil moisture showed a strong influence on soil and microbial respiration, while soil temperature had strong influences on soil and root respiration (Fig. 6). Since soil temperature and moisture, and aboveground biomass were correlated, we conducted multiple regression analysis. Results showed soil, microbial and root respiration was influenced by not only soil physical environmental (i.e. soil temperature and moisture), but also plant growth (i.e. aboveground biomass) (Table 5). Soil temperature, soil moisture and aboveground biomass together explained 84%, 76% and 74% of total soil respiration, microbial and root respiration, respectively.

When individual measurements of soil, microbial and root respirations and temperature were used and separated into different precipitation treatments, nonlinear relationships of soil respiration and soil temperature ( $<30^\circ\text{C}$ ) were revealed (Fig. 7). It is noticeable that above  $30^\circ\text{C}$ , soil respiration tended to decline and these data were not included in the models. The soil temperature sensitivities of soil, microbial and root respirations were generally higher in wet treatments than in the ambient and drought treatments. Temperature sensitivity of soil respiration did not change much among the ambient, and two drought treatments, but was higher under the +50% treatment (2.83). The  $Q_{10}$  values of microbial respiration in the +50% treatment were



**Fig. 4** Relationships of soil, microbial, and root respirations with precipitation change in 2014 and 2015. Each point represents mean of all measurements for the treatment. Simulated precipitation is the total water added to the plot for each treatment in one year. Model parameter estimations are presented in Table 3

**Table 3** Linear regression of soil, microbial, and root respiration and simulate precipitation in two years and among three different harvest periods

Year or harvest period	Respiration measurement	Intercept	Slope	Standard error	95% Confidence interval	r <sup>2</sup>	t test
2014	Soil	0.402	0.00253a	0.000092	0.00224 ~ 0.00282	0.996**	
	Microbial	0.197	0.00184a	0.000161	0.00133 ~ 0.00235	0.978**	
	Root	0.090	0.00130a	0.000387	0.00065 ~ 0.00253	0.789*	2.88*
2015	Soil	-0.088	0.00444b	0.000316	0.00344 ~ 0.00545	0.985**	
	Microbial	-0.124	0.00292a	0.000674	0.00077 ~ 0.00506	0.862*	
	Root	0.271	0.00064a	0.000191	0.00003 ~ 0.00125	0.788*	7.28**
1	Soil	0.092	0.04299a	0.003350	0.03232 ~ 0.05365	0.982**	
	Microbial	-0.045	0.03303a	0.005540	0.01540 ~ 0.05067	0.922**	
	Root	0.106	0.01421a	0.006920	-0.00782 ~ 0.03623	0.584	4.74**
2	Soil	0.389	0.07909b	0.009190	0.04985 ~ 0.10833	0.961**	
	Microbial	0.163	0.05819b	0.008550	0.03100 ~ 0.08539	0.929**	
	Root	0.286	0.02396b	0.004100	0.01092 ~ 0.03701	0.919**	8.07**
3	Soil	0.107	0.03703a	0.002110	0.03032 ~ 0.04374	0.990**	
	Microbial	0.064	0.02632a	0.002390	0.01870 ~ 0.03393	0.976**	
	Root	0.126	0.00948a	0.002930	0.00016 ~ 0.01880	0.778*	9.96**

Between the two years or among three harvest periods, slopes of soil, microbial or root respiration labeled with the same letter are not significant based on homogeneity of slope test. r<sup>2</sup>: coefficient of determination. t test is used to test significant difference in slopes between microbial respiration and root respiration

Stars indicate the level of significance (\* =  $p < 0.05$ , \*\* =  $p < 0.01$ )

relative higher (2.67), but Q<sub>10</sub> of root respiration was higher in the +33% treatment (2.89). The Q<sub>10</sub> values of soil and microbial respiration between ambient and drought treatments were similar.

## Discussion

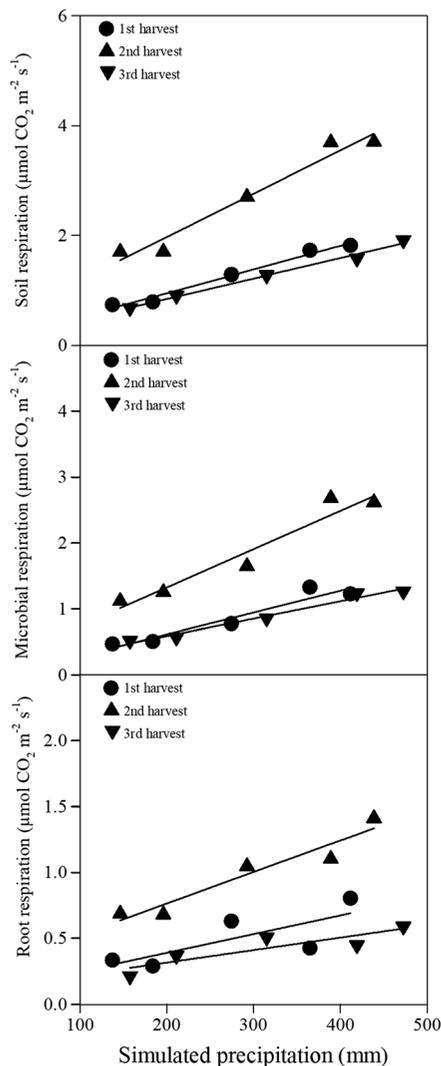
Measuring soil respiration in switchgrass soils in big pots under the five different precipitation treatments over two years, we found that soil, microbial and root respiration rates increased with wet treatments and decreased with dry treatments. Soil respiration was mostly

contributed by soil microbial respiration. Soil microbial respiration was also more sensitive to precipitation change than root respiration. Across all treatments, soil, microbial and root respiration rates were significantly influenced by soil temperature, soil moisture, tiller height, and aboveground biomass. We do not know whether belowground biomass was better correlated to respiration rate as no destructive root biomass measurement was made in this study. Base soil respiration rate and temperature sensitivities of soil, microbial and root respiration of switchgrass were influenced by precipitation treatments. These information improved our understanding of soil respiration in switchgrass soils and

**Table 4** Multiple comparisons of soil, microbial and root respiration rates among three different harvest periods

Harvest period	Soil respiration ( $\mu\text{mol CO}_2\text{m}^{-2}\text{ s}^{-1}$ )	Microbial respiration ( $\mu\text{mol CO}_2\text{m}^{-2}\text{ s}^{-1}$ )	Root respiration ( $\mu\text{mol CO}_2\text{m}^{-2}\text{ s}^{-1}$ )
Feb-April	1.26 ± 0.06 <sup>a</sup>	0.81 ± 0.03 <sup>a</sup>	0.50 ± 0.03 <sup>a</sup>
May-July	2.70 ± 0.09 <sup>b</sup>	1.78 ± 0.06 <sup>b</sup>	0.99 ± 0.10 <sup>b</sup>
August-Nov.	1.27 ± 0.11 <sup>a</sup>	0.86 ± 0.03 <sup>a</sup>	0.43 ± 0.05 <sup>a</sup>

Data are mean ± SE. The sample size is 150 for soil respiration and 90 for microbial and root respiration. LSD is used for multiple comparison among means. Different letters indicate significant differences between the harvest periods



**Fig. 5** Relationships of soil, microbial, and root respirations with precipitation change during three harvest periods. Each point represents mean of all measurements for the treatment. Simulated precipitation is the total water added to the plot for each treatment within each harvest period. Model parameter estimations are presented in Table 3

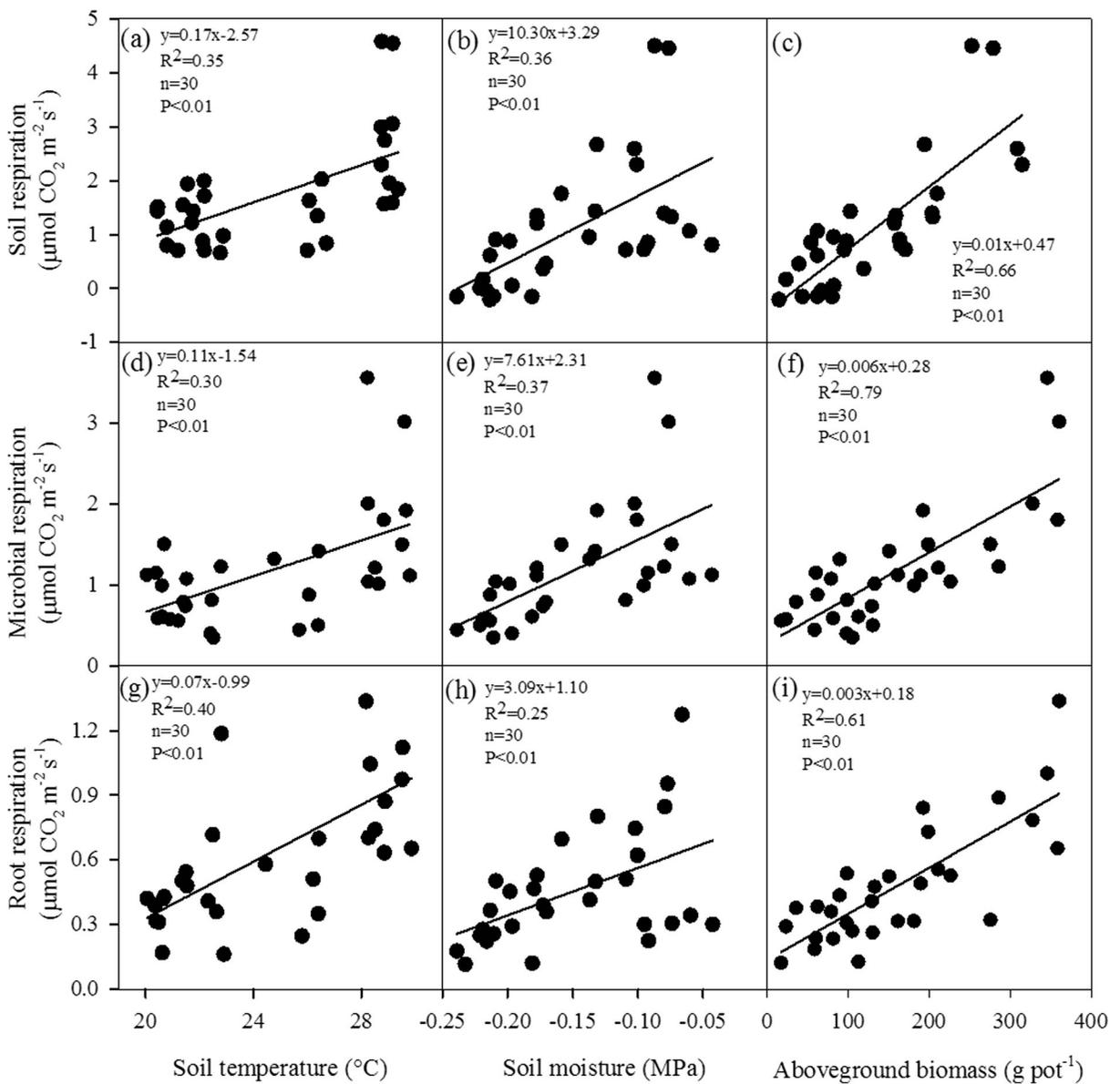
could be useful for ecosystem modeling of soil respiration in the future.

Responses of soil, microbial and root respiration rates to precipitation treatments

About 40% increase in soil respiration in the +50% treatment and 40% decrease in the -50% treatment were found compared to the ambient treatment in this study (Fig. 3). These results were supported by some previous experiments that reported increases in soil respiration

under water addition and decreases under water reduction (Deng et al. 2012; Jiang et al. 2013; Wagle and Kakani 2014; Vicca et al. 2014). The magnitudes of soil respiration changes were comparable to some previous studies in grasslands. For example, soil respiration was increased by 31% in an arid and semiarid grassland with 30% increase in annual precipitation (Liu et al. 2009). A drought treatment which reduced annual precipitation by 66% caused a 25% decrease in soil respiration in a mesic grassland (Hoover et al. 2016). The enhanced soil respiration in our study was mostly due to the increases in microbial respiration in the wet treatments, while drought treatments equally reduced microbial and root respiration (Fig. 3). It seems that there was more soil carbon decomposition in the wet treatments. Our result of 40% reduction in microbial respiration in the drought treatments was higher than that in Suseela et al. (2012). The reduction of microbial respiration could be mostly caused by changes in soil water content that influencing diffusivity of soluble substrates and soil microbial communities (Zhou et al. 2009; Cregger et al. 2012). The reduced root respiration in the drought treatments were supported by reduced growth of switchgrass in our study (Fig. 6).

The significant differences in soil, microbial and root respirations between two years and among harvest periods could be related to differences in soil temperature and plant growth between two years and among these harvest periods. The average of soil temperature was lower during the 1st and 3rd harvest period than during the 2nd harvest period, and caused lower soil respiration (Figs. 1 and 2). Similar seasonal variations have been reported before. For example, Lee et al. (2007) reported that soil respiration increased as soil temperature increased, and reached maximum fluxes from July through August. Maximum daily soil CO<sub>2</sub> flux is 6.09 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> for the control switchgrass plots, higher than we observed in our study. In addition, a 4-year experiment showed the daily microbial and root respiration during the growth period ranged from 0.6 to 4.7, and 0 to 4 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>, respectively (Anderson-Teixeira et al. 2013). Seasonal variations of soil respiration could also be related to plant development and soil moisture conditions (Fig. 6). Plant photosynthesis or growth can directly influence soil respiration (Saleska et al. 1999; Dornbush and Raich, 2006; Huang et al. 2016). Other studies in grasslands also showed that differences in above-ground biomass



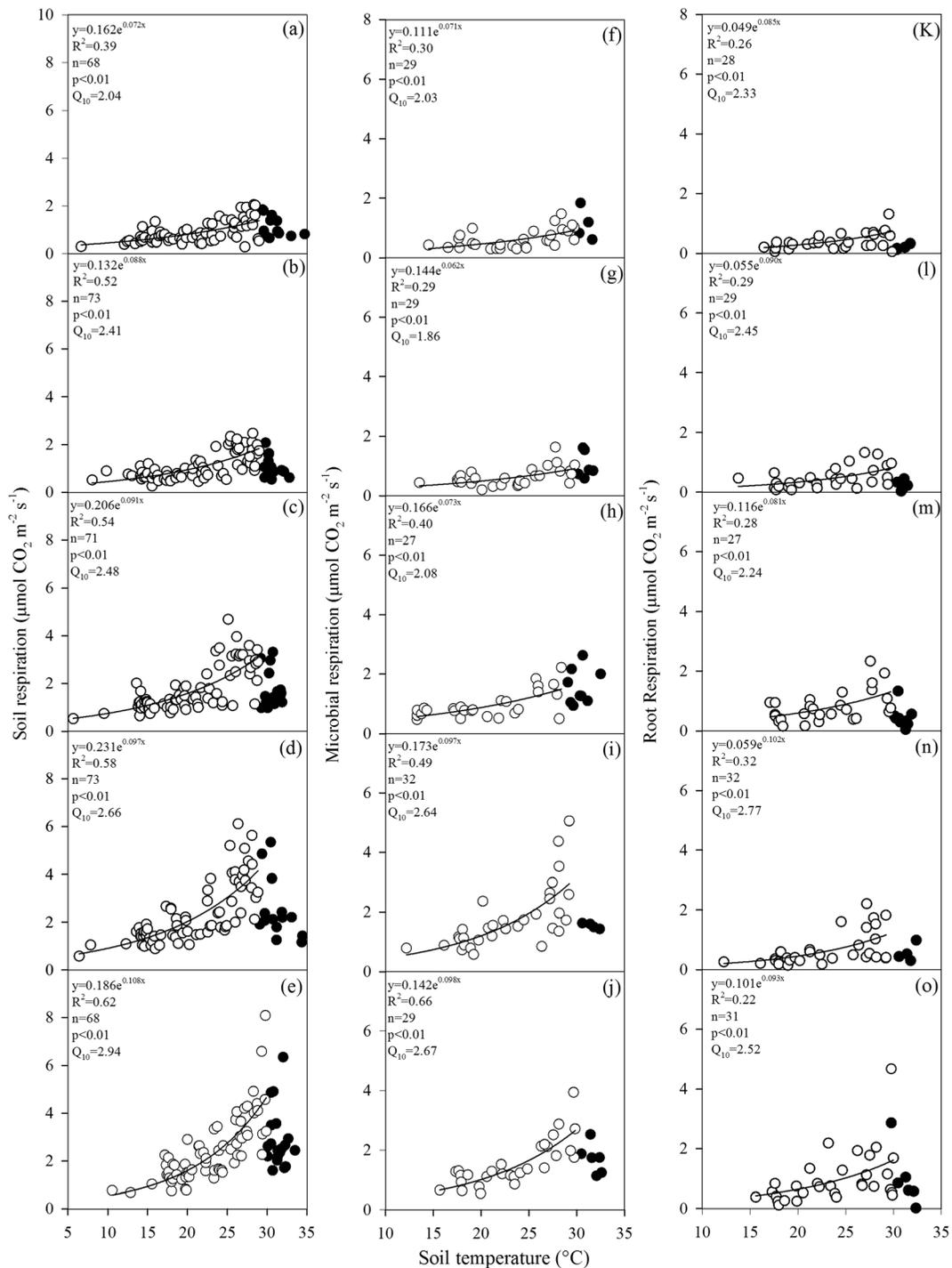
**Fig. 6** Relationships of soil, microbial, and root respirations with soil temperature, soil moisture, and plant growth under the five precipitation treatments. Each data point represents mean value of each period

**Table 5** Relationships of soil respiration and its components with plant growth, soil temperature, and soil moisture under all precipitation treatments

Response variable	Model	R <sup>2</sup>
Soil Respiration	$R = -1.1320 + 0.0090\text{Msoil} + 0.1543\text{Tsoil} + 0.0028\text{B}$	0.84**
Microbial Respiration	$R = -0.30 + 6.04\text{Msoil} + 0.08\text{Tsoil} + 0.002\text{B}$	0.76**
Root respiration	$R = -0.5463 + 0.0017\text{Msoil} + 0.0499\text{Tsoil} + 0.0016\text{B}$	0.70**

Ms.: soil moisture; Ts: soil temperature; B: aboveground of biomass. Mean values of three harvest periods of two years are used. Sample size is 85 for soil respiration and 34 for microbial and root respiration

Stars indicate the level of significance (\* =  $p < 0.05$ , \*\* =  $p < 0.01$ )



**Fig. 7** Relationships of soil, microbial and root respirations with soil temperature under the  $-50\%$  (a, f, k),  $-33\%$  (b, g, l), Ambient (c, h, m),  $+33\%$  (d, i, n) and  $+50\%$  (e, j, o) precipitation treatments. Panels a, b, c, d, and e are soil respiration; f,

g, h, i and j are microbial respiration; and k, l, m, n and o are root respiration. The black points represent the respiration measured at soil temperature above  $30\text{ }^\circ\text{C}$  that are excluded for temperature sensitivity estimations

significantly influence soil respiration and its components (Bahn et al. 2009; Byrne and Kiely 2006; Craine and Wedin 2002; Wagle and Kakani 2014).

Precipitation sensitivity of soil, microbial and root respiration rates between years and among harvest times

Based on linear regression model between respiration and precipitation amount, we developed precipitation sensitivity of respiration using the slope of the model. We found that precipitation sensitivity of microbial respiration was higher than root respiration, indicating that decomposition of soil organic C by soil microbes is more sensitive to precipitation change than root activity in switchgrass soils (Wang et al. 2015). More CO<sub>2</sub> would be emitted through organic C decomposition than root respiration in the wet years (Linn and Doran 1984).

Precipitation sensitivity also varied between years and among harvest periods. In the warmer year or period, soil microbial and total soil respirations were more sensitive to precipitation change. The reason could be that high temperature stimulated more microbial growth and activity. With adequate water availability, more organic C could be decomposed. Indeed, both microbial and soil respiration rates were higher in 2015 than 2014, and in 2nd harvest period than the 1st and 3rd harvest periods (Fig. 2).

The form of the relationship between soil respiration and precipitation/soil moisture can vary, as both linear and nonlinear responses have been reported (Luo and Zhou 2006; Zhou et al. 2006; Sponseller 2007; Deng et al. 2012). In our study, total soil, microbial and root respirations generally linearly increased with precipitation (Figs. 4, 5). But we noticed that soil microbial respiration tended to level off or even decline at the highest precipitation treatment, probably due to limitation of O<sub>2</sub> concentration in the wet soil to soil microbial activity (Linn and Doran, 1984). Total and soil microbial respirations also did not differ much at the two drought conditions, indicating that there might be threshold precipitation values those limiting soil total and microbial respirations. Studies with more precipitation levels are needed to investigate their relationships in the future.

Responses of temperature sensitivities of soil, microbial and root respirations to precipitation treatments

Significant relations between respiration and temperature were developed for soil, microbial and root

respiration ( $P < 0.01$ ) after excluding data points beyond 30 °C. We found that soil, microbial and root respiration rates dropped when soil temperature was higher than 30 °C. Influences of soil moisture on temperature sensitivities of soil respiration have been reported in grasslands (Bouma et al. 1997; Suseela et al. 2012; Liu et al. 2016). For example, Suseela and Dukes (2013) found that Q<sub>10</sub> value (1.71) in grassland under the -50% precipitation treatment is lower than under the ambient precipitation (1.93) and the +50% precipitation treatment (2.07). In our study, Q<sub>10</sub> values of soil respiration at the +33% and +50% treatments were 2.66 and 2.94, which was similar to the result (2.7) in semi-arid grasslands of North Dakota (Frank 2002) and (2.7) in a tall grass prairie of Oklahoma (Luo et al. 2001). One recent meta-analysis (Liu et al. 2016) showed that if the precipitation amount is 28% more than the ambient level, the temperature sensitivity of soil respiration (Q<sub>10</sub>) value increases by about 6%. Our results showed that the Q<sub>10</sub> at the +33% and 50% treatments were increased by 7.2% and 18.5%, respectively. In contrast, the low and no significant difference of Q<sub>10</sub> of soil microbial and root respiration between the ambient and drought treatments could be due to the suppressions of root activity and low C substrate inputs to the soil in the water limited conditions (Suseela et al. 2012; Liu et al. 2016).

## Conclusion

Using a two-year greenhouse precipitation experiment in Nashville, TN, we demonstrated that soil, microbial and root respiration rates of switchgrass were significantly influenced by precipitation treatments. Increases in precipitation mostly stimulated microbial respiration while decreases in precipitation reduced both microbial and root respirations. Soil, microbial and root respiration rates were significantly correlated with soil moisture, soil temperature, and aboveground biomass across all treatments. Precipitation sensitivity of soil microbial respiration was significantly higher than root respiration, indicating that increasing precipitation could stimulate more decomposition of soil organic C than it might stimulate root respiration. Soil temperature sensitivities of soil, microbial and root respiration increased more in the wet treatments than those decreased in the drought treatments compared to the ambient precipitation. These results indicate that high temperature and more

precipitation would stimulate more CO<sub>2</sub> emissions in switchgrass soils, while C losses will be slowed by drought. These changes have potentially significant implications for the prediction of soil C budget in biofuel switchgrass lands under long term precipitation change conditions.

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